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THE SPORE-FORMING SPECIES OF THE GENUS SACCHAROMYCES.

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In his monograph on the *Saccharomycetaceae* [*Saccardo*: Sylloge Fungorum omnium hucusque cognitorum, Vol.VIII, page 916–22.] *J. B. de Toni* enumerated 31 species of the genus *Saccharomyces* Meyen upon which the family is based by *Reess* in the year 1870, when it was separated from the *Ascomycetes*. Since *DeToni's* monograph was published, our knowledge of this important family, among which very important culture plants are found, has been widely broadened, mainly by the investigations of *Emil Chr. Hansen*, so that several species may be added to those already known. But further *De Toni*, in his monograph, has given no notice to the species described and figured by *Hansen*, nor to the extensive literature based upon these. We find in the "Sylloge" species as *Saccharomyces ellipsoideus* Reess, *S. conglomeratus* Reess, *S. Pasteurianus* Reess, and the description of the species is based solely upon the morphology of the cells. In fact, for the description not only reliable morphological but purely physiological characters of these fungi have been used and must to a certain extent be used. *Reess* and other mycologists before *Hansen* and his school have taken in consideration for the description almost solely the morphological characters of the cells; but we may easily observe that the form and size, etc., of the cells have very little to do with the species question. The latter depends much more upon the number of spores found in the cells, the conditions for the spore-formation, and the effect upon the various kinds of sugar. As therefore *De Toni's* monograph can not pretend to give a correct account of the species known up to date, I have tried to bring together the forms in which a formation of spores has been found, with description of the various stages in their development. A later number of this series, materials for a monograph on the alcoholic fermentation, will contain the literature in full.

Fungaceae. Linné, Gen. 1737, page 327.

SACCHAROMYCETACEAE. Reess.

M. Reess: Botanische Untersuchungen ueber die Alkoholgaehrungspilze, 1870. Winter: Die Pilze (in Rabenhorst's Kryptogamenflora)I, 1, page 68. *Blastomycetes* Frank: Leunis Synopsis, Botanik, III, page 595.

Genus: *Saccharomyces.* Meyen.

Meyen: Wiegmann's Archiv. Vol. IV. 2, page 100, 1838. Reess, l. c. Winter, l. c., page 69. Joergensen, Die Mikroorganismen der Gaehrungsindustrie, 1890, page 123. Saccardo, Sylloge, VIII, page 916 [De Toni.]. Ludwig: Lehrbuch der niederen Kryptogamen, 1892, page 210.

All species unicellular, often adhering together, forming a false mycelium. Hyphae or regular mycelia never occur. Cells circular, oval, or ellipsoid, often rectangular. *Habitat:* Causing the conversion of glycose into alcohol and carbonic acid, and a few other products, most of the species are always found in fermenting fluids. Some species are found in other places, most of these, however, have not been observed forming spores. Further investigation must determine the true nature of the latter; probably some of them belong to the Torula-forms in the sense of Pasteur. Owing to the general feeling that the Saccharomyces are characterized mainly by their faculty of spore-formation, I took up only these forms in the present synopsis.

Propagation by buds. This is the general way of propagation. Where a vigorous conversion of sugar is caused by the Saccharomyces, an equal rapidity of the budding is always observed.

Propagation by spores. In all of the species mentioned here a spore-formation has been traced and investigated, and many species are based upon the conditions for this formation, which *Hansen* has found constant in all the forms described and studied by him.—Form of spores round or oval, in one species, "hat-formed;" their number 1–10 or more. Appearance various in the various species, also transparency. Spores invariably endogenous.

Appearance of the colonies. When cultivated in a 10 per cent. beer-wort-gelatine the colonies appear as round or oval, white macroscopic spots, the outline of which is even in some, uneven in other species.—Cultivation for spore-formation, see *Hansen:* Meddelelser fra Carlsberg-Laboratoriet. Vol. II, page 152; *Holm* and *Poulsen,* ibidem page 218. (Compte Rendus, etc., Carlsberg. II, page 97; *Holm and Poulsen,* ibid, page 141.) 1886–88.—For the formation of a top-vegetation see each single species.

1. Saccharomyces cerevisiae I. Hansen.

Hansen, l. c. II, page 67; Plate I, fig. 1; Pl. III, fig. 1–3.

Sacch. cerevisiae Meyen (ex parte) Wiegm. Arch. IV, page 109; Reess Unters. page 81; Pl. 1, fig. 1–17; Pl. II, fig. 1–6. Winter: Pilze. I, 2, page 69, and fig. Joergensen Mikroorg. 1890, page 124. Ludwig, l. c. page 215.

Torula cerevisiae Turpin: Mém. de l'Académie XVII, 1840, page 93; Plate I- , Comptes Rendus de l'Acad. Vol. VII, 1838, page 369 (without plates.), Liebigs Annalen XXIX, page 93. Kuetzing: Journal fuer prakt. Chemie Vol. XI, page 387, 1837, and plate.—Cryptococcus cerevisiae Kuetz.: Phycol. gener. page 148, 1843; Cryptococcus cerevisiae Kuetz, Species Algarum, page 146, 1849.—Hormiscium cerevisiae Bail in Flora 1857, page 417. Pasteur: Ann. d. Phys. et de Chim. LXII, page 332–426. id. Etudes sur la bière, page 185–192, 1876. Garnier: Ferments et Fermentations Paris, 1888, page 75.

This form and many varieties of it is common in breweries. The specific form gives a top-fermentation. Cells 2, 5 μ–6μ; the young culture gives mainly round and slightly oval, or ellipsoid cells. Spore-formation found: Maximum: 36°–37° C., minimum 11°–12°C. The first trace of spores at 25° C. found in 23 hours, at 15° C. in 72 hours. Number of spores generally 1–4, of round shape and of strong reflecting power.

In giving a key to the determination of the species, it seems best to select the occurrence of spore-formation by 25° and 15°, not only because this is most instructive but also because these temperatures are used for examination of the yeast in the breweries, the physiological yeast-analysis; another reason is that it enables the investigator to keep two thermostates at the points 25° and 15° as long as the investigation lasts. The very best apparatus for these investigations is, of course, the Panum thermostate, described by Pedersen in Meddelelser fra Carlsberg-Laboratoriet, Vol. I, page 48–52, 1878, or by Panum in Nordisk medic. Arkiv. Vol. X, No. 4.

This species and its varieties, which are cultivated for constant use in brewing establishments are known as "cultivated yeasts," the other forms, which cause "sickness" in the product, being commonly called "wild yeasts." In these cultivated forms, the spores are very refractive, compared with the other forms, and their spore-forming cells often display a singular formation of a thick wall which divides the cell into various parts, each of these containing a spore. This "wall" is very refractive and consists of the protoplasm of the cell, pressed in between the walls of the spores. But the same formation may also appear as a result of the spores being pressed against each other. Occasionally there is a real formation of a wall, when the spores cannot be separated, and then the cell turns out to be a kind of a sporangium.

A superficial layer of cells which we will call top-vegetation occurs at 3°–5° C. never after 7–10 days at 20–22° C. This kind of vegetation generally gives cells of a singular shape.

Among the many varieties found in breweries all over the world all cannot be sure to give the same results; but the question of variation has still to be debated.

2. Saccharomyces Pastorianus I. Hansen.

Hansen, l. c. II, page 68; Plate I, fig. 2; Pl. V, fig. 1–3.—S. Pastorianus Reess, l. c. page 83; Pl. II, fig. 11–13 (ex parte.). Winter, l. c. page 70. Saccardo, l. c. page 917. Pasteur: Etudes sur la bière, 1876, page 150, fig. 128, Pl. X–XI, page 171–75, fig. 33–37, Pl. XII (ex parte.). Garnier, l. c. page 78. Joergensen, l. c. page 127. Ludwig, l. c. page 215.

Often found in the cellars where the fermentation of the beer takes place; it gives a bottom- fermentation. A young culture in beer-wort gives round and oval, sausage-formed cells; the spores are formed at 27°, 5 in 24 hours, at 15° in 50 hours, maximum being at 29°, 5–30°, 5, minimum at 3°–4°. Number of spores 1–5, commonly 5–10 are also found, their diameter being 1.5–5μ.

Top-vegetation does not occur at 34°, but in 8–15 days at 20°–22°; it gives cells of irregular shape, long, sausage-formed, as well as small, round and oval cells. Gives the beer a very bitter taste.

3. Saccharomyces Pastorianus II. Hansen.

Hansen, l. c. page 69; Pl. I, fig. 3; Pl. V, fig. 1–3. Other references under the preceding species (ex parte.). Joergensen, l. c. page 129. Ludwig, l. c. page 215.

Common in the air in the brewery, consequently often found in the fermenting beer. Cells round or long oval. Spore-formation: 25° in 25 h., 15° in 48 h. Maximum 27°–28°, minimum 3°–4°. Spores like those of the preceding, wall-formation sometimes found.

Gives a weak top-fermentation. Top-vegetation gives, when the culture is young, a large number of small, round or oval cells, when old, we find long, irregular shaped forms; not found at 34°, at 20°–22° in 8–15 days.—Gelatine-cultures give round, even-edged colonies.

4. Saccharomyces Pastorianus III. Hansen.

Hansen l. c. II, page 70, Pl. II, fig. 1; Pl. VI, fig. 1–3. See preceding. Joergeusen, l. c. page 130. Ludwig, l. c. page 216.

Found causing a peculiar disease in the yeast. Gives a well marked bottom-fermentation. Cells long, oval and ellipsoid. Spore-formation: 25° in 28 h., 15° in 35 h. Max. 27°–28°; Min. 4°. Top-vegetation never found at 34°, occurs in 9–12 days at 20°–22°, the culture giving, when old, very irregular, almost thread-shape cells.—Gelatine-culture has round colonies with fringed edges.

5. *Saccharomyces ellipsoideus I.* Hansen.

Hansen, l. c. II, page 71; Pl. III, fig. 2; Pl. VII, fig. 1–3.

S. ellipsoideus Reess, l. c. page 82; Pl. III, fig 1–7. Pasteur, l. c. page 242, fig. 58. Joergensen, l. c. page 132. Ludwig, l. c. page 216. [" Wine-yeast."]

Found on the surface of grapes. Cells round, oval, ellipsoid; gives bottom-fermentation. Spore formation: 25° in 21 hours. 15° in 45 h.; maxim. 30°, 5–31°, 5; minim. 7°, 5. Top-vegetation gives always round and oval, scarcely long and irregular cells, does not occur at 38°, but at 20°–22° in 10–17 days.

5. *Saccharomyces ellipsoideus II.* Hansen.

Hansen, l. c. II, page 71; Pl. II, fig. 3; Plate VIII, fig. 1–3. Reess, Pasteur loci cit. Joergensen, l. c. page 135. Ludwig, l. c. page 216.

Found together with S. Pastorianus III in diseased yeast. Gives sometimes top-, sometimes bottom-fermentation. Cells similar to those of S. ellipsoideus I. Spore-formation: 25° in 27 h., 15° in 70 h. Max. 33°–34°; min. 8°.—Young top vegetation gives round and oval cells, occurs never at 40°, at 20°–22° in 4–6 days; the old vegetation has long cells, and a mycelium-like appearance.

7. *Saccharomyces Marxianus.* Hansen.

Hansen: Annales de Micrographie, 1888, Nr. 2–3, page 3, l. c. page 222, Joergensen, l. c. page 136. Ludwig, l. c. page 219.

Found on grapes. In beer-wort it gives a number of elliptic, egg-formed cells, and later small colonies of mycelium-like growth. Spores not easily formed, the latter being generally round or slightly oval, but often kidney-shaped. Top-vegetation scarce. On gelatine a "false" mycelium is often formed.

8. Saccharomyces exiguus. Hansen.

Hansen: Annal. d. Microgr. 1888, Nr. 2–3, page 5; l. c. II, page 225. [Reess, l. c. page 82; Pl. II, fig. 7–8, and Hansen, l. c. I, page 227. (ex parte.)]. Saccardo, Sylloge, VIII, page 917, 1889. Joergensen, l. c. page 136. Ludwig, l. c. page 220. Winter, Pilze, I, page 70 (ex parte.).

Probably a distinct species. In beer-wort good development and often formation of a "yeast-ring." Cells 2–5μ, round and oval, scarcely long.—Found in press-yeast. Spores rare, top-vegetation seldom occurs. No mycelial growth in fluids.

9. Saccharomyces membranaefaciens. Hansen.

Hansen: Ann. d. Micr., l. c. page 6; l. c. II, page 225. Saccardo, l. c. page 918. Joergensen, l. c. page 137. Ludwig, l. c. page 220.

Found on decaying elm-roots. Gives in beer-wort abundant top-vegetation of oval cells. Spores easily formed both in cultures in fluid and in spore-cultures. Gelatine-cultures show reddish colonies, the substratum being slowly liquefied.

10. Saccharomyces Ludwigii. Hansen.

Hansen, Centralbl. f. Bakteriol. u. Paras. V, page 638, 1889; Meddel. III, page 62, 1891. Joergensen, l. c. page 138. Ludwig, l. c. page 218.

Found in "Schleimflüsse" of oak-trees. Cells elliptical, flask-formed, or long and irregular shaped. On gelatine a mycelium is developed, with branches and septa. Cultures in fluids give spores abundantly. Power of variation great, some forms easily giving spores, while others do not. Germination of spores peculiar; see Hansen, Medd. III, page 62–70. 1891.

11. Saccharomyces anomalus. Hansen.

Hansen, l. c. III, page 71. Ludwig, l. c. page 219.

In impure yeast from brewery and on grapes. Cells round and oval, rarely long. Spores formed both in the bottom-yeast and in the top-vegetation, they are " hat-shaped," a form not occurring in any other species.

12. Saccharomyces Hansenii. Zopf.

Zopf: Berichte der Deutschen bot. Gesellschaft, Vol. VI, page 94–97; 1889, with figures.

Found in cotton-dust. Spores 1–2 in each cell, ball-formed, diam. 2–4μ. This species does not give rise to alcoholic fermentation, but it brings fermentation in a solution of saccharose, dextrose, lactose, galactose, maltose, mannit, dulcit, and glycerin, converting these sugars and the glycerin into oxalic acid, the latter being found at the bottom of the solution as calcium oxalate when the fermentation is at an end.

13. Saccharomyces Joergensenii. Lasché.

Lasché: Der Braumeister, Vol. V, page 242–245. Chicago, 1892; and Zeitschrift f. d. gesammte Baruwesen, Munich 1892. With figures.

Found in "temperance-beer." Cells 2.5–5.5μ. Spore-formation: 26° in 20 h., 25° in 17 h., 12° in 4 days. Maxim. 28°–30°, Min. 8°: "wall "-fermation in the spore-forming cells scarce. Causes no disease in the beer. Gelatine-cultures give a " false mycelium."

[*14. Saccharomyces conglomeratus.* Reess.

Reess, l. c. page 82; Pl. II, fig. 14–16. Winter, l. c. page 70. Saccardo, l. c. VIII, page 917. Joergensen, l. c. page 140.

Cells 5–6μ. Typical forms appear with more than one bud on the propagating cell. It is hardly a distinct species, because such forms often are found in old cultures by Hansen, Will, and other investigators,[1] mainly in top-vegetation.]

15. Saccharomyces albicans. Reess.

Reess; Sitzungsberichte d. phys. med. Gesellschaft Erlangen. 1877. Winter, l. c. page 72.

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[1] For example, see Will's figures.

Oidium albicans Robin (Histoire naturelle d. vég. parasit. page 488; pl. I, fig. 3–7.)

Cells round and oval, found in the mouth of small children. Number of spores one. Has been considered the same as Sacch. mycoderma (Mycod. cerevisiae) which forms no spores and therefore is probably no Saccharomyces.

16. Saccharomyces Reessi. David.

David: Annalen der Oenologie IV, page 223, 1878.

Found in wine-fermentation. Cells form three spores. Almost unknown.

17. Saccharomyces galacticola. Pirot. and Rib.

Pirotta and Riboni: Studii sul latte, page 14, pl. VI, fig. 6; pl. XVII, fig. 1, 1879.

Occurs in "fermenting" milk where it forms smaller rows, sometimes a short mycelium. Cells with 2–4 spores.

18. Saccharomyces I of Will.

Will: Zeitschrift f. d. gesammte Brauwesen. No. 7–8. 1891.

In beer; the taste of the product becomes very much affected. Cells oval or of a pastorian form. The top-vegetation has long cells and a "false mycelium," when old. The old bottom-yeast forms short rows, similar to those cultivated varieties which give top-fermentation. Spore-formation: 25° in 14, 5 h.; 15° in 41 h. Max. 41°; min. 4°–5°. Top-vegetation: 41° never; 22°–23° in 4–6 days. "Conglomeratus"-forms (see No. 14) figured.

19. Saccharomyces II of Will.

Will l. c.

Habitat as the preceding form. Spores: 24°, 5–25° in 31 h.; 15°–15° 5 in 74 h.; diam. 2–4μ, number: 1–4. Max. 32°; min. 0°, 5–1°. Top-vegetation found, often developing into the formation of a yeast-ring.

20. Saccharomyces minor. Engel.

Engel: Les ferments alcooliques, 1872. Arcangeli: Nuovo giorn. bot. Ital, 1888, page 303. Joergensen, l. c. page 139.

Sphaerous cells, diam. 6μ. Short rows. Spore-forming cells 7–8μ; spores 2–4, diam. 3μ.

21. Saccharomyces Ilicis. Groenlund.

Groenlund: Zeitschr. f. d. gesammte Brauwesen, 1892, page 289, with fig., and Videnskabelige Meddelelser f. d. naturhist. Foren. i Kjoebenhavn, Vol. LIV, page 5, 1893.

Found on fruits of Ilex aquifolium. Cells round, similar to Sacch. cerev. I. Spore-formation: 25° in 22 h., 15°. 5 in 3 days. Max. 36°–37°; min. 9°. 5.—Bottom-fermentation. Top-vegetation found after 122 or 165 days in the temperature of the room, in sunlight after 93 days. Gives the beer a disagreeable, bitter taste.

22. Saccharomyces Aquifolii. Groenlund.

Groenlund, l. c., page 297; Vid. Medd., page 9.

On Ilex-fruits. Cells larger than those of the preceding. Spores: 25°, 5–26°, 5 in 29 h.; 16° in 3½ days. Max. 27° 5–28°, 5; min. 10°–10°, 5. Gives the beer a sweet-bitter taste. Top-fermentation.

CONCLUDING REMARKS.

If we were able to trace the *Saccharomycetaceae* back into their history, we should be able to form an opinion with regard to their origin. But, for the present time, there is no reason whatever for regarding these organisms as a form of some fungi of higher organization which have been subject to a one-sided evolution. We have never seen a *Saccharomyces* develop into anything but a *Saccharomyces*.

The term "fermentation" is hardly to be used any more. Originally, in the sense of *Liebig*, it meant the conversion of carbo-hydrates into products of a lower combination, terminating in the formation of CO_2 and H_2O, by means of the life-activity of lower organisms (the theory of vitality). Now, however, it is also applied to the *conversion of proteid substances* by means of a life-activity. Since the enzymes have been found and studied, it would be more proper to speak of the conversion of such and such matter into certain products

I. THE CONDITION OF THE SPORE-FORMATION AND OF TOP-VEGETATION.

Temp.	S. cerevisiae I.		S. Pastor I.		S. Pastor II.		S. Pastor III.		S. ellips. I.		S. ellip, II.	
°C.	Spore-f.	Top-veg.	Spore-f.	Top-veg.	Spore-f.	Top-veg.	Spore-f.	Top-veg.	Spore-f.	Top-veg.	Spore-f.	Top-veg.
40.°												0.
38.										0.		—
37	0 ; 29 h.											
35											0.	
34		—; max.		0.		0.		0.		—	—; 31 h.	
32									} 0.			
31				} 0.					} —; 36 h.			
30	Opt. 20h .			} —; 30 h.					} —23 h.			
29			—; 27 h.		0.		0.				Opt.; 22 h.	
28				—	—; 34 h.	—	—; 35 h.	—				
27			Opt.; 24 h.									
25	—; 23 h.		—; 24-26 h.		Opt.: 25 h.		Opt.; 28 h.		—; 21 h.	—; 10-17 d.	—; 27 h.	—; 4-6 d.
20–22		7-10 d.		—; 8-15 d.		—; 8-15 d.		—; 9-12 d.		—; 15-30 d.		—; 8-10 d.
13–15		15-30 d.		—; 15-30 d.		—; 10-25 d.		—; 10-20 d.				
11	—; 10 d.	—; 10 d.										
9	0.											
8							—; 9 d.				—; 9 d.	
7										—		
5		0.		—		—		—		0.		—
4			— } 14 d.		— } 17 d.		0.		0.		0.	
3			— }		— }							
2				0.		0.		0.				0.
0.5.					0.							

0 signifies no growth.
— signifies that the process takes place.

h. hours.
d. days.

II. ACTION OF THE SPORE-FORMING SACCHAROMYCES ON DIFFERENT KINDS OF SUGAR.

	$C_6H_{12}O_6$	Invert sugar formed and the invertin fermented.	$C_{12}H_{22}O_{11}$	Maltose.	Lactose.
S. cerevisiae I. S. Pastorianus I–III. S. ellipsoideus I–II. S. Ilicis ; S. aquifolii.	0.	—	—	—	0.
S. Marxianus ; S. exiguus. S. Joergensenii; S. Ludwigii.	0.	—	—	0.	0.

0 signifies no fermentation; — signifies a fermentation.

III. SIZE AND NUMBER OF SPORES.

No.	Spores.		No.	Spores.	
used above.	Diameter.	Number.	used above.	Diameter.	Number.
1	2,5–6μ.	1– 5.	12		
2	1,5–5μ.	1–10.	13	1-2,5μ.	2–4.
3	2–5μ.	1– 7.	14		
4	2–4μ.	1–10.	15		1.
5	2–4μ.	1– 4.	16		3.
6	2–5μ.	1– 4.	17		2–4.
7	2–4μ.		18	1,5–5μ.	1–5.
8	2–4μ.	2– 3.	19	2–4μ.	1–4.
9			20	3.	2–4.
10		1– 8.	21		
11		2– 4.	22		

through the life-activity of this or that organism, or enzyme, and this mode of expression would also indicate more about the process than the terms fermentation or putrefaction are able to do.

The names yeast or yeast-fungi ought to be used exclusively on the species of Saccharomycetes, not including the mycoderma (cerevisiae and vini—Saccharomyces mycoderma), Torula, and those of the moulds which give either no fermentation or a fermentation (conversion of glucose) with a large per cent. of alcohol. And, finally, the genus Saccharomyces should comprise only the spore-forming species.

MISSOURI BOTANICAL GARDENS, May, 1893.